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Visceral organ mass in wethers consuming diets with different forages and grain levels [1]

B. Kouakou [a], A.L. Goetsch [b,*], A.R. Patil [a], D.L. Galloway, Sr. [a], K.K. Park [a]

[a] *Department of Animal Science, University of Arkansas, Fayetteville, AR 72701, USA*

[b] *South Central Family Farm Research Center, Agricultural Research Service, USDA, Booneville, AR 72927-9214, USA*

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Abstract

Crossbred wethers (72; 33 ± 0.6 kg live weight) were used to investigate interactions among forage source, cereal grain inclusion and level, and length of feeding on visceral tissue mass. Wethers consumed long-stemmed alfalfa ((A) *Medicago sativa*; early bloom), bermudagrass ((B) *Cynodon dactylon*; 6 to 8 weeks of regrowth) or ryegrass (*Lolium multiflorum*; early head emergence)-wheat (*Triticum aestivum*; anthesis (RW)) hay and approximately 0, 20 or 40% ground corn (0, 20 and 40, respectively) for 49 or 98 d. Digestible organic matter intake ranked ($P < 0.05$) B < RW < A and was increased ($P < 0.05$) by grain inclusion (period 1: 0.62, 0.75, 0.73, 0.28, 0.45, 0.49, 0.57, 0.57 and 0.69 kg/d; period 2: 0.73, 0.91, 0.96, 0.30, 0.49, 0.56, 0.55, 0.73 and 0.91 kg/d); mean empty body weight was 37, 40, 40, 34, 35, 36, 36, 38 and 39 kg (SE 1.2) for A-0, A-20, A-40, B-0, B-20, B-40, RW-0, RW-20 and RW-40, respectively. Total gastrointestinal tract tissue mass was lower ($P < 0.06$) for B than for A or RW (1.98, 2.11, 1.97, 1.69, 1.78, 1.78, 1.84, 1.93 and 1.95 kg), and epithelium comprised a greater ($P < 0.05$) proportion of ventral ruminal tissue for A versus RW or B (25, 27, 27, 19, 22, 21, 20, 25 and 21% for A-0, A-20, A-40, B-0, B-20, B-40, RW-0, RW-20 and RW-40, respectively). Liver mass was 0.48, 0.51, 0.57, 0.34, 0.40, 0.40, 0.41, 0.49 and 0.44 kg in period 1 (SE 0.037), and 0.53, 0.56, 0.49, 0.38, 0.41, 0.41, 0.42, 0.43 and 0.51 kg in period 2 (SE 0.022) for A-0, A-20, A-40, B-0, B-20, B-40, RW-0, RW-20 and RW-40, respectively. In conclusion, cereal grain inclusion increased digestible organic matter intake and decreased gastrointestinal tract and liver mass relative to digestible organic matter intake similarly regardless of forage source, grain level or feeding period length. Thus, effects of cereal grain inclusion on peripheral tissue energy availability should be greater than expected based on digestible organic matter intake and, relative to conditions without supplemental grain, such differences should decrease with increasing forage quality and feeding period length as digestible organic matter intake increases. © 1997 Elsevier Science B.V.

Keywords: Sheep; Forage; Visceral tissues; Splanchnic

1. Introduction

Cereal grains are common supplements of forages used to improve performance. Means by which this occurs include increased total tract organic matter digestibility and a decrease in forage intake that is

* Corresponding author.

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usually less than grain consumption. However, effects of cereal grains on forage intake and digestion vary among forage sources and grain levels (Jarrige et al., 1986; Orskov and Ryle, 1990).

Efficiency of energy metabolism with restricted feed intake is directly related to dietary concentrate level and differs among forage sources with metabolizability (Agricultural Research Council, 1980; National Research Council, 1984). However, recently it was proposed that under practical production conditions ad libitum intake by growing beef steers and lactating dairy cows varies with dietary quality or metabolizability so that efficiency of whole-body energy metabolism is relatively constant (Tolkamp and Ketelaars, 1994). The gastrointestinal tract and liver together account for approximately one-half of whole-body heat production, although this proportion varies with experimental or production conditions (Ferrell, 1988). Recent studies indicate that splanchnic bed oxygen consumption relative to digestible energy intake with forage-based diets consumed ad libitum decreases as digestible energy intake increases in response to different forage qualities and dietary concentrate levels (Goetsch et al., 1994; Goetsch and Ferrell, 1995; Patil et al., 1995; Goetsch et al., 1996a; Goetsch et al., 1996b). Thus, assuming constant whole-body efficiency of energy metabolism with ad libitum feed intake, efficiency of energy metabolism in extra-splanchnic tissues may decrease as digestible or metabolizable energy intake increases and as the proportion of absorbed energy reaching peripheral tissues increases. This implies potential impact on ad libitum intake and (or) visceral tissue mass of animal characteristics, such as affected by length of the feeding period, through influences on the capacity for or fate of acetate metabolism in peripheral tissues (Leng et al., 1993; Scollan and Jessop, 1995). Therefore, interactions among forage characteristics, supplemental grain inclusion and level, and length of feeding on mass of metabolically active tissues, feed intake and digestibility are possible. Objectives of the present experiment were to investigate the potential for such interactions among forage source (i.e., legume and tropical and temperate grasses), dietary cereal grain inclusion and level (0, 20 and 40% of dry matter), and feeding period length (49 or 98 d) on visceral tissue mass in growing wethers.

2. Materials and methods

2.1. Animals

Shorn wethers (72, 33 ± 0.6 kg initial full body weight, Rambouillet × Dorset and approximately 4 months of age) were used in an experiment with a 3×3 factorial arrangement of treatments. Wethers were weighed (full) on consecutive days at the beginning, middle and end of the 98 d experiment, with two 49 d periods. Based on the first weight at the beginning of the study, wethers were allotted to 18 groups (four per group) to achieve similar mean body weight (BW) and variation in BW within group. Groups were randomly assigned to treatments, and each was housed in a 1.6×1.9 m pen situated in a wooden building with free access to water. Thus, each group in a pen consisted of four wethers. Wethers were dewormed before the experiment.

2.2. Diets

Wethers consumed long-stemmed alfalfa ((A) *Medicago sativa*; early bloom), bermudagrass ((B) *Cynodon dactylon*; 6 to 8 weeks of regrowth) or ryegrass (*Lolium multiflorum*; early head emergence)-wheat (*Triticum aestivum*; anthesis (RW)) hay ad libitum with approximately 0, 20 or 40% ground corn (0, 20 and 40, respectively). Actual quantities of corn offered were slightly greater than 20 and 40%. Corn was completely consumed, and some hay was present at the end of each day. Quantities of feedstuffs offered were varied daily so that hay refused would be 5 to 10% of that offered on the preceding few days. All wethers received a basal supplement (Table 1) at 0.3% BW (dry matter), which minimized differences in dietary concentration of crude protein. Meals were at 08.00 h daily, with supplement, corn and hay fed sequentially after weighing and removal of orts. Hay was sampled daily during the last 2 weeks of each 49 d period to form composites, and concentrates were sampled once each of the last 2 weeks for period composites. Hay samples were ground to pass a 1 mm screen.

2.3. Sampling and analyses

On d 41 through 44 in period 1 and on d 90 through 93 in period 2, grab fecal samples were

Table 1
Supplement composition (%; air-dry basis)

Item	Dietary forage source		
	Alfalfa	Bermudagrass	Ryegrass-wheat
Ground corn	93.87	1.37	50.83
Soybean meal		48.33	19.32
Blood meal		14.77	5.91
Corn gluten meal		19.25	7.70
Salt	1.34	1.37	1.37
Dicalcium phosphate	3.88	5.79	5.76
Calcium carbonate		8.23	8.19
Trace mineral premix [a]	0.45	0.46	0.46
Vitamin premix [b]	0.30	0.31	0.30
Lasalocid premix [c]	0.16	0.16	0.16

[a] Contained > 12% Zn, 10% Mn, 5% K, 2.5% Mg, 1.5% Cu, 0.3% I, 0.1% Co and 0.02% Se.
[b] Contained 8.8 million IU of vitamin A, 0.9 million IU of vitamin D_3 and 1100 IU of vitamin E/kg (air-dry basis).
[c] To supply lasalocid at approximately 1 mg/kg body weight.

obtained at 12 h intervals, advancing 3 h daily, from two wethers per pen chosen randomly in period 1. Samples were composited (fresh weight basis) within animal, dried at 55°C and ground to pass a 1 mm screen. Ruminal fluid was collected by stomach tube from the wethers used for fecal collections at 4 and 8 h post-feeding on d 45 and 93.

Composite samples of feed and feces were ground through a 1 mm screen and analyzed for dry matter (DM), ash, Kjeldahl nitrogen (N; Association of Official Analytical Chemists, 1984), neutral detergent fiber ((NDF) Goering and Van Soest, 1970; without decalin, ethoxyethanol or sodium sulfite) and acid insoluble ash (Van Keulen and Young, 1977; 2 *N* HCl). For concentrate NDF analysis, subsamples were ground to pass a 0.6 mm screen and treated with amylase (Cherney et al., 1989). Composition of feces averaged across animals within a pen and average pen feed intake (3 d prior to and on days of fecal sampling) were used to calculate digestibilities, with use of acid insoluble ash as an internal, indigestible marker. In addition, feed samples were analyzed for acid detergent fiber and lignin (Goering and Van Soest, 1970). Ruminal fluid was analyzed for volatile fatty acids (Goetsch and Galyean, 1983) and ammonia N (Broderick and Kang, 1980).

Thirty-six wethers (those used earlier in a period for fecal and ruminal fluid samples) were slaughtered and eviscerated daily on the 4 d following periods 1 and 2 (nine per day and one per treatment). Organs were tied at junctions, separated and weighed. Gastrointestinal tract components were the reticulo-rumen, omasum, abomasum, small intestine, cecum and large intestine. Other tissues included the liver, heart, lungs, spleen, kidneys and visceral fat. Digesta was removed from gastrointestinal tract (GIT) segments; the reticulo-rumen, omasum, abomasum, cecum and large intestine were washed with tap water and residual water was removed; and empty tissue and digesta mass were determined. Subsamples of mixed reticulo-ruminal and small intestinal digesta samples were obtained, dried at 55°C, ground to pass a 1 mm screen and analyzed for DM, ash and NDF. Empty BW was determined by subtracting digesta mass from full BW measured immediately before slaughter.

Tissue sections of mid-dorsal and -ventral areas of the rumen, proximal duodenum, mid-jejunum, mid-ileum, mid-large intestine and liver were excised immediately after evisceration. Tissue samples were individually wrapped in aluminum foil, labelled and frozen in liquid nitrogen for storage (−72°C). Intestinal samples were later allowed to thaw, cut and weighed after removal of residual digesta. Gastrointestinal tract sections were then separated into epithelial and nonepithelial components by scraping with a microscope slide, with the proportion of epithelial tissue (fresh weight basis) determined as the difference between total and nonepithelial tissue mass

2.4. Statistical analyses

Data were analyzed as a split-plot design, with 49 d period as the subplot, by general linear models procedures of Statistical Analysis System (1990). The model consisted of forage source, grain treatment, forage source by grain treatment interaction, group within treatment (error for previous variation sources), period, and two-way and three-way interactions between period and forage source and (or) grain treatment. The number of observations was 36, derived from 18 pens and two periods. Data from each period were analyzed separately when an interaction involving period was significant ($P < 0.05$), with 18 observations per period. When the forage

source by grain treatment interaction was nonsignificant ($P > 0.05$), differences among forage source were determined by least significant difference when the F-value was significant ($P < 0.05$). Likewise, with a nonsignificant ($P > 0.05$) forage source by grain treatment interaction, orthogonal contrasts for grain inclusion (0 versus 20 and 40%) and non-zero grain level (20 versus 40%) were conducted. Differences among forage source-grain treatments were determined by least significant difference when the interaction between forage source and grain treatment was significant ($P < 0.05$). Simple correlation coefficients were determined; regressions were performed with general linear models and regression procedures of Statistical Analysis System (1990).

3. Results

Because of real differences in composition or variability in feedstuff sampling procedures, concentrations of chemical constituents in forage sources were not identical in both periods. Alfalfa was 20 and 22% crude protein and 52 and 47% NDF in periods 1 and 2, respectively. Bermudagrass was similar between periods in concentrations of crude protein and NDF, although RW was 67 and 60% NDF in periods 1 and 2, respectively. The mean crude protein concentration was greater in A than in B or RW (Table 2). Neutral detergent fiber and acid detergent lignin concentrations differed among forage sources as expected with forages of similar relative stages of maturity (Minson, 1990), ranking A < RW < B and A > B > RW, respectively.

Table 2
Feedstuff composition

Item	Alfalfa	Bermuda-grass	Ryegrass-wheat	Corn
Ash	7.1	8.3	8.0	1.5
Crude protein	20.7	11.7	12.0	13.2
Neutral detergent fiber	49.2	69.2	63.5	9.5
Acid detergent fiber	39.2	35.2	35.9	
Acid detergent lignin	8.5	5.3	4.2	
Cellulose	30.7	29.9	31.7	
Hemicellulose	13.5	34.6	29.8	

Hay intake in period 1 was affected by an interaction ($P < 0.05$) between forage source and grain treatment (Table 3). In period 1, hay intake was similar for A and RW, greater ($P < 0.05$) for A versus B, and greater ($P < 0.05$) for RW than for B with 0 and 20% grain. Most responsible for the interaction was a tendency for decreasing hay intake as grain level increased with A and RW but numerically greater hay intake for 20 versus 0% grain with B. In period 2, intake of B was less ($P < 0.05$) than that of A or RW, decreased ($P < 0.05$) with grain inclusion, and was less ($P < 0.05$) for 40 versus 20% grain. Total DM intake in both periods was less ($P < 0.05$) for B than for A and with than without corn.

Digestibilities varied ($P < 0.05$) with period but interactions between period and dietary treatments were not observed ($P > 0.05$). In part, period effects may have resulted from aforementioned differences in forage composition. Also, the low number of animals per pen and coupling of average chemical composition of feces from one-half of animals in period 1 with average intake of all animals in a pen may have contributed to period effects. Therefore, digestibilities averaged across periods were discussed rather than differences between periods.

Organic matter digestibility ranked ($P < 0.05$) B < RW < A and 0 < 20 < 40% grain (Table 3). Neutral detergent fiber digestibility was less ($P < 0.05$) for B than for A or RW and was similar among grain treatments ($P > 0.05$). Total tract apparent N digestibility was lower ($P < 0.05$) for RW than for A or B. Digestible OM intake in both periods ranked ($P < 0.05$) B < RW < A and was increased ($P < 0.05$) by grain inclusion. An interaction ($P < 0.05$) between period and grain treatment was elicited by greater ($P = 0.08$) digestible OM intake for 40 versus 20% grain in period 2 but similar intake in period 1.

Differences among treatments in ruminal fluid ammonia N concentration (Table 4) occurred (RW < B < A and 0 < 20 and 40% grain; $P < 0.05$), but magnitudes of difference were not substantial. The concentration of total volatile fatty acids in ruminal fluid was greater ($P < 0.05$) for A versus B or RW and greater for 40 versus 20% grain in period 1; in period 2, total volatile fatty acid concentration ranked ($P < 0.05$) RW < B < A and was increased ($P <$

0.05) by grain inclusion. The acetate to propionate ratio was similar among treatments in period 2 ($P > 0.05$), although in period 1 the ratio was less for A versus B or RW and greater ($P < 0.05$) for 20% grain than for 0 or 40%. The molar percentage of butyrate was greater ($P < 0.05$) for A versus B or

Table 3
Intake and digestion by wethers consuming diets with different forages and grain levels

Item	Alfalfa			Bermudagrass			Ryegrass-wheat			SE	Effect [a]
	0 [b]	20 [b]	40 [b]	0	20	40	0	20	40		
Dry matter intake (g/d)											
Supplement	100	109	105	104	108	109	104	104	107	2.64	
Corn											
Period 1 [c]	0	207	406	0	143	278	0	183	296	23.8	B < A, B < RW; I, L
Period 2 [c]	0	267	501	0	172	319	0	235	547	40.2	B < A, B < RW; I, L
Hay											
Period 1	969 [i]	823 [h,i]	609 [f,g]	443 [d,e]	566 [e,f]	397 [d]	849 [h,i]	719 [g,h]	585 [e,f,g]	46.0	
Period 2	971	824	610	444	534	349	850	720	586	49.5	B < A, B < RW; I, L
Total											
Period 1	1068	1129	1114	545	811	778	949	1004	1081	66.2	B < A, B < RW; I
Period 2	1073	1209	1221	550	821	784	959	1062	1249	84.8	B < A, B < RW; I
Organic matter											
Intake (g/d)											
Period 1	992	1060	1057	484	737	716	861	924	1009	62.5	B < A, B < RW; I
Period 2	994	1136	1161	488	748	724	875	986	1177	80.5	B < A, B < RW; I
Digestion											
%	67.6	75.2	76.2	58.8	62.9	72.8	64.5	67.9	72.5	1.63	B < RW < A; I, L
g/d											
Period 1	617	749	733	277	445	486	565	574	686	47.3	B < RW < A; I
Period 2	726	905	960	298	493	564	554	726	907	64.3	B < RW < A; I
Neutral detergent fiber											
Intake (g/d)											
Period 1	505	450	360	314	413	309	577	508	438	28.8	B < A < RW; I, L
Period 2	468	425	345	309	388	275	515	460	409	30.9	B < A, B < RW; L
Digestion											
%	56.1	62.7	57.1	53.3	51.2	52.7	62.9	60.6	57.2	2.27	B < A, B < RW
g/d											
Period 1	258	266	173	165	207	147	390	292	239	22.7	B < A < RW; I, L
Period 2	287	282	227	171	204	160	300	292	246	23.1	B < A, B < RW; L
Nitrogen											
Intake (g/d)											
Period 1	32.1	32.0	29.5	18.3	23.6	23.4	22.7	23.9	25.6	1.70	B < A, RW < A
Period 2	35.8	36.6	33.9	19.5	25.7	25.3	20.3	22.9	27.5	2.24	B < A, RW < A
Digestion											
%	72.3	72.4	68.9	72.5	68.5	75.5	56.8	56.7	62.1	1.71	B < A, RW < B
g/d											
Period 1	21.1 [h]	20.7 [g,h]	17.2 [f,g]	12.8 [d,e]	15.2 [d,e,f]	16.2 [e,f]	13.3 [d,e]	12.2 [d]	14.8	1.10	
Period 2	28.3	29.2	26.7	14.6	18.7	20.7	11.2	14.3	18.2	1.63	RW < B < A; I

A = alfalfa; B = bermudagrass; RW = ryegrass-wheat.

[a] < denotes a difference ($P < 0.05$) between forage sources; I = grain inclusion (0 versus 20 and 40%; $P < 0.05$); L = grain level (20 versus 40%; $P < 0.05$).

[b] Approximate dietary grain level (%).

[c] 49 d.

[d,e,f,g,h,i] Means in a row without a common superscript differ ($P < 0.05$).

RW and generally increased with increasing grain level.

Total GIT digesta mass was similar ($P > 0.05$) among treatments in period 1; however, GIT digesta mass in period 2 was greater ($P < 0.05$) for B than for A or RW and was decreased ($P < 0.05$) by grain inclusion (Table 5). These differences were primarily consequences of corresponding ones in reticulo-ruminal and omasal digesta mass. Digesta mass in the abomasum, cecum and large intestine was similar ($P > 0.05$) among treatments; whereas, small intestinal digesta mass was less ($P < 0.05$) for RW versus A or B and decreased ($P < 0.05$) with dietary grain inclusion.

Ash concentration in ruminal digesta was less ($P < 0.05$) for A than for RW or B (Table 5). Concentration of NDF in ruminal digesta was similar among treatments (Table 5). Small intestinal digesta ash concentration was lower for A than for B or RW ($P < 0.05$), and an effect ($P = 0.08$) of grain inclusion on intestinal digesta ash concentration existed as well.

Empty BW was 37, 40, 40, 34, 35, 36, 36, 38 and 39 kg (SE 1.2), and BW gain was 86, 116, 101, 35, 49, 51, 72, 78 and 110 g/d (SE 11.1) for A-0, A-20, A-40, B-0, B-20, B-40, RW-0, RW-20 and RW-40, respectively. Total GIT mass was lower ($P < 0.05$) for B than for A or RW diets, which was elicited by similar but largely nonsignificant ($P > 0.05$) differences in mass of component tissues (Table 6). The only effect ($P < 0.05$) of grain treatment noted was one of inclusion on large intestinal tissue mass. Expressed as a percentage of empty BW, forage treatment did not affect total GIT tissue mass; whereas, GIT tissue mass was decreased ($P < 0.05$) by grain inclusion and was lower ($P = 0.08$) for 40 versus 20% grain (6.48, 6.13, 5.74, 6.43, 6.26, 6.12, 6.13, 6.10 and 5.87% for A-0, A-20, A-40, B-0, B-20, B-40, RW-0, RW-20 and RW-40, respectively; SE 0.158). Interactions between period and dietary

Table 4
Ruminal fluid NH_3–N and volatile fatty acid concentrations in wethers consuming diets with different forages and grain levels

Item	Alfalfa			Bermudagrass			Ryegrass-wheat			SE	Effect [a]
	0 [b]	20 [b]	40 [b]	0	20	40	0	20	40		
NH_3–N (mg/dL)	10.0	8.1	9.1	6.2	7.9	5.8	5.8	6.2	5.1	0.47	RW < B < A
Volatile fatty acids											
Total (mM/L)											
Period 1 [c]	92.4	86.0	101.1	86.0	75.7	80.8	78.3	80.0	81.9	3.29	B < A, RW < A; L
Period 2 [c]	101.2	113.5	100.6	93.2	95.6	97.1	82.4	90.1	92.2	2.93	RW < B < A; I
Molar %											
Acetate	61.7	60.7	57.5	66.5	65.7	62.4	66.0	63.0	61.8	0.96	A < B, A < RW; I, L
Propionate											
Period 1	24.3	21.0	24.7	22.8	21.6	23.3	23.9	21.6	21.3	0.76	I, L
Period 2	24.0	23.0	21.8	22.1	23.0	22.9	22.8	24.1	22.8	0.94	
Isobutyrate	0.79	0.74	0.93	0.73	0.67	0.70	0.41	0.62	0.59	0.135	
Butyrate	10.6 [e,f]	14.8 [h]	15.3 [h]	8.5 [d]	9.3 [d,e]	11.4 [f,g]	8.7 [d]	10.7 [f]	12.5 [g]	0.42	I, L
Isovalerate	1.57	0.83	1.34	1.23	1.33	1.44	0.88	2.00	2.14	0.561	
Valerate	1.12	0.93	1.62	0.73	0.76	0.95	0.69	0.78	0.93	0.084	B < A, RW < A; I, L
Acetate:propionate											
Period 1	2.53	2.94	2.32	2.89	3.07	2.66	2.72	2.97	2.92	0.136	A < B, A < RW; L
Period 2	2.62	2.63	2.72	3.06	2.88	2.79	2.99	2.64	2.79	0.129	

A = alfalfa; B = bermudagrass; RW = ryegrass-wheat; NH_3–N = ammonia nitrogen.

[a] < denotes a difference ($P < 0.05$) between forage sources; I = grain inclusion (0 versus 20 and 40%; $P < 0.05$); L = grain level (20 versus 40%; $P < 0.05$).

[b] Approximate dietary grain level (%).

[c] 49 d.

[d,e,f,g,h] Means in a row without a common superscript differ ($P < 0.05$).

Table 5
Digesta mass and composition in wethers consuming diets with different forages and grain levels

Digestive tract segment	Alfalfa			Bermudagrass			Ryegrass-wheat			SE	Effect [a]
	0 [b]	20 [b]	40 [b]	0	20	40	0	20	40		
Reticulo-rumen (fresh g)											
Period 1 [c]	4190	3337	4232	4451	4495	4593	4391	4385	3827	560.8	
Period 2 [c]	3982	3795	2938	6518	5161	5211	4903	4021	4032	390.2	A < RW < B; I
Omasum (fresh g)											
Period 1	110	98	91	102	123	132	88	79	72	21.8	
Period 2	130	109	72	219	140	212	110	91	99	17.7	A < B, RW < B; I
Abomasum (fresh g)	167	134	193	173	165	213	144	170	137	38.1	
Small intestine (fresh g)	565	469	376	528	458	521	494	407	297	33.7	RW < A, RW < B; I
Cecum (fresh g)	277	286	244	256	317	257	253	223	218	44.4	
Large intestine (fresh g)	637	606	538	622	625	605	567	598	484	50.0	
Total (fresh g)											
Period 1	6124	4860	5875	5979	6109	6339	5848	6092	5160	715.5	
Period 2	5580	5468	4160	8466	6938	7003	6560	5280	5143	496.0	A < B, RW < B; I
Ruminal digesta											
Ash (% DM)	10.1	9.5	9.9	11.4	10.6	10.6	10.5	10.5	11.3	0.56	
NDF (% DM)	67.5	65.7	65.0	66.8	64.7	66.9	65.2	61.9	63.6	1.83	
Small intestinal digesta											
Ash (% DM)	13.3	12.5	12.6	15.2	14.3	14.5	14.8	13.6	13.7	0.66	A < B, A < RW
NDF (% DM)											
Period 1	38.4	25.8	19.0	38.4	26.8	36.9	36.5	26.4	25.8	3.46	I
Period 2	28.1	30.4	23.5	31.9	30.3	28.6	30.4	22.0	22.5	3.38	

A = alfalfa; B = bermudagrass; RW = ryegrass-wheat; DM = dry matter; NDF = neutral detergent fiber.
[a] < denotes a difference ($P < 0.05$) between forage sources; I = grain inclusion (0 versus 20 and 40%; $P < 0.05$).
[b] Approximate dietary grain level (%).
[c] 49 d.

Table 6
Gastrointestinal tract tissue mass (fresh; g) in wethers consuming diets with different forages and grain levels

Digestive tract segment	Alfalfa			Bermudagrass			Ryegrass-wheat			SE	Effect [a]
	0 [b]	20 [b]	40 [b]	0	20	40	0	20	40		
Reticulo-rumen	647	683	640	608	599	598	664	650	655	34.1	
Omasum	79	73	71	70	67	84	69	72	67	7.2	
Abomasum	139	150	145	120	133	133	127	145	132	5.7	B < A
Small intestine	719	776	726	580	624	593	621	658	709	44.8	B < A
Cecum	39	39	41	28	37	33	36	34	35	3.2	
Large intestine	360	383	347	281	315	338	317	374	350	19.9	B < A; I
Total	1982	2105	1969	1686	1775	1779	1835	1932	1949	87.3	B < A, B < RW

A = alfalfa; B = bermudagrass; RW = ryegrass-wheat.
[a] < denotes a difference ($P < 0.05$) between forage sources; I = grain inclusion (0 versus 20 and 40%; $P < 0.05$).
[b] Approximate dietary grain level (%).

Table 7
Percentage of epithelium (fresh weight) in gastrointestinal tract tissues in wethers consuming diets with different forages and grain levels

Item	Alfalfa			Bermudagrass			Ryegrass-wheat			SE	Effect [a]
	0 [b]	20 [b]	40 [b]	0	20	40	0	20	40		
Ventral rumen	25.3	27.1	26.9	18.9	22.4	21.4	19.7	25.0	20.9	2.24	B < A, RW < A
Dorsal rumen											
Period 1 [c]	18.4	23.4	20.3	22.2	16.3	23.9	18.1	18.9	23.5	1.98	
Period 2 [c]	31.3	29.4	28.7	19.5	22.6	23.9	22.3	21.3	24.5	1.89	B < A, RW < A
Duodenum	65.8	66.4	65.1	65.6	61.7	64.9	62.8	65.2	68.7	2.21	
Jejunum											
Period 1	83.9	82.4	79.3	82.5	78.5	80.2	84.9	80.9	86.8	1.71	
Period 2	81.1	81.2	84.2	84.8	79.6	82.6	85.1	79.7	84.3	1.70	I
Ileum											
Period 1	75.2 [f,g]	71.2 [e,f,g]	71.1 [e,f,g]	68.7 [e,f]	67.0 [d,e]	60.5 [d]	71.3 [e,f,g]	61.2 [d]	77.4 [g]	2.22	
Period 2	62.6	55.7	75.3	64.0	57.8	61.4	65.1	61.5	65.8	2.86	L
Large intestine	43.8	44.9	40.6	44.1	41.2	42.0	40.4	42.3	43.6	1.58	

A = alfalfa; B = bermudagrass; RW = ryegrass-wheat.
[a] < denotes a difference ($P < 0.05$) between forage sources; I = grain inclusion (0 versus 20 and 40%; $P < 0.05$); L = grain level (20 versus 40%; $P < 0.05$).
[b] Approximate dietary grain level (%).
[c] 49 d.
[d,e,f,g] Means in a row without a common superscript differ ($P < 0.05$).

treatments in total GIT mass as a percentage of empty BW did not occur; however, a difference ($P < 0.05$) between periods existed (6.59 and 5.69% for periods 1 and 2, respectively; SE 0.114).

The proportion of epithelial tissue in the ventral rumen was greater ($P < 0.05$) for A versus B or RW diets (Table 7), and a similar effect ($P < 0.05$) was observed in period 2 for the dorsal rumen. The proportion of duodenal epithelial tissue was similar ($P > 0.05$) between periods and among treatments. Proportions of epithelium in the jejunum and ileum varied among treatments differently ($P < 0.05$) in

Table 8
Mass (fresh; g) of internal organs and visceral fat in wethers consuming diets with different forages and grain levels

Item	Alfalfa			Bermudagrass			Ryegrass-wheat			SE	Effect [a]
	0 [b]	20 [b]	40 [b]	0	20	40	0	20	40		
Liver											
Period 1 [c]	484	510	566	338	395	401	406	491	442	37.3	B < RW < A
Period 2 [c]	528	562	491	378	413	413	419	431	505	21.6	B < RW < A
Heart	181	193	197	157	165	172	179	193	177	6.3	B < A, B < RW; I
Lungs	424	424	462	373	389	409	435	430	441	19.7	B < A, B < RW
Spleen	62	76	68	47	57	57	60	63	62	5.4	B < A
Kidneys	93	99	96	84	84	84	92	90	94	4.7	B < A
Visceral fat	846	1347	1303	542	728	839	763	902	1182	111.5	B < RW < A; I

A = alfalfa; B = bermudagrass; RW = ryegrass-wheat.
[a] < denotes a difference ($P < 0.05$) between forage sources; I = grain inclusion (0 versus 20 and 40%; $P < 0.05$).
[b] Approximate dietary grain level (%).
[c] 49 d.

Table 9
Mass (fresh) of gastrointestinal tract tissues and the liver relative to digestible organic matter intake (g/g) in wethers consuming diets with different forages and grain levels

Item	Alfalfa			Bermudagrass			Ryegrass-wheat			SE	Effect [a]
	0 [b]	20 [b]	40 [b]	0	20	40	0	20	40		
Reticulo-rumen											
Period 1 [c]	1.00 [d,e]	0.85 [d]	0.86 [d,e]	1.98 [f]	1.22 [e]	1.15 [d,e]	1.12 [d,e]	1.15 [d,e]	0.87 [d,e]	0.114	
Period 2 [c]	0.93 [d,e,f]	0.81 [d,e]	0.69 [d]	2.34 [h]	1.36 [g]	1.13 [e,f,g]	1.26 [f,g]	0.88 [d,e,f]	0.78 [d,e]	0.131	
Omasum	0.117	0.089	0.088	0.251	0.143	0.160	0.123	0.111	0.086	0.0204	A < B, RW < B; I
Abomasum	0.209 [d,e]	0.181 [d]	0.175 [d]	0.425 [g]	0.288 [f]	0.253 [e,f]	0.228 [d,e,f]	0.228 [d,e,f]	0.166 [d]	0.0213	
Small intestine	1.08	0.95	0.89	2.08	1.35	1.15	1.11	1.04	0.91	0.133	A < B, RW < B; I
Cecum	0.059	0.048	0.050	0.100	0.080	0.063	0.065	0.054	0.045	0.0086	A < B, RW < B; I
Large intestine	0.537	0.463	0.421	1.011	0.678	0.646	0.565	0.586	0.444	0.0732	A < B, RW < B; I
Total gut	2.97	2.56	2.40	6.03	3.83	3.41	3.28	3.04	2.48	0.356	A < B, RW < B; I
Liver											
Period 1	0.787	0.681	0.772	1.270	0.888	0.820	0.720	0.857	0.645	0.0984	A < B, RW < B
Period 2	0.728	0.621	0.516	1.289	0.858	0.734	0.757	0.595	0.558	0.0634	A < B, RW < B; I

A = alfalfa; B = bermudagrass; RW = ryegrass-wheat.
[a] < denotes a difference ($P < 0.05$) between forage sources; I = grain inclusion (0 versus 20 and 40%; $P < 0.05$).
[b] Approximate dietary grain level (%).
[c] 49 d.
[d,e,f,g,h] Means in a row without a common superscript differ ($P < 0.05$).

periods 1 and 2, although treatment differences for the large intestine were similar between periods. Proportions of epithelial tissue in the ventral rumen (25.5 versus 20.6%) and large intestine (45.6 versus 39.5%) were greater ($P < 0.05$) in period 1 than in period 2.

Liver mass (Table 8) ranked ($P < 0.05$) B < RW < A in both periods. Mass of other organs were either less ($P < 0.05$) for B than for A or less ($P < 0.05$) than for both A and RW. As a percentage of empty BW, liver mass was greater ($P < 0.05$) for A than for B or RW diets (1.64, 1.55, 1.54, 1.36, 1.43, 1.40, 1.37, 1.49 and 1.42% for A-0, A-20, A-40, B-0, B-20, B-40, RW-0, RW-20 and RW-40, respectively; SE 0.054) and lower ($P < 0.05$) for period 2 versus 1 (1.36 versus 1.57%; SE 0.029). Visceral fat mass ranked ($P < 0.05$) B < RW < A and was increased ($P < 0.05$) by grain inclusion.

An interaction ($P < 0.05$) existed between forage source and grain treatment in the ratio of reticulo-ruminal tissue mass to digestible OM intake in both periods (Table 9). The total GIT ratio was greatest ($P < 0.05$) among forage sources for B and was decreased ($P < 0.05$) by grain inclusion. Similar differences ($P < 0.05$) among forage sources in the ratio of liver mass to digestible OM intake were noted in both periods; liver mass:digestible OM intake was decreased by grain inclusion in period 1 ($P = 0.08$) and in period 2 ($P < 0.05$).

4. Discussion

Factors responsible for differences among treatments in digesta mass cannot be conclusively discerned from these data. One might rationalize such differences solely through physical and chemical characteristics of feedstuffs (e.g., NDF concentration). However, an explanation based on physiological control of intake, with digesta mass in the GIT being the end-result of both intake and physical and chemical feedstuff characteristics, also is possible. In regards to physical properties with either line of thought, Wilson (1993) suggested that the 'girder' structure of tropical grass fragments, entailing plant tissues with protruding and jagged edges, leads to entanglement in the ruminal digesta mat, which contributes to slow ruminal digesta exit and increased digesta mass. Such factors may have accounted for greatest digesta mass among forage sources for B in

the present experiment. The high density of grain particles immediately after ingestion, more rapid ruminal digestion of grain than forage, and small particle size of masticated grain probably contributed to lower digesta mass in the reticulo-rumen and total GIT for 0 versus 20 or 40% grain diets.

Lower saliva flow for A than for B or RW diets because of less mastication per unit DM of ingested legume than grass (Moseley and Dellow, 1985; Grenet, 1989) may explain the lower concentration of ash in ruminal and intestinal digesta. Lowest concentrations of digesta ash for A imply lower physiological workload associated with mineral absorption. Dietary grain level also was expected to affect mastication but did not elicit comparable change in digesta ash concentration.

Tissue mass provided an indication of differences among treatments in quantities of energy and nutrients consumed by visceral tissues. There is a positive relationship between GIT and liver mass and associated energy expenditures (Ferrell et al., 1986; Johnson et al., 1990). However, proportions of visceral tissue energy use, with practical production conditions, attributable to tissue mass versus metabolic activity per unit of tissue mass have not been elucidated. Results of Burrin et al. (1990) with growing sheep consuming a high concentrate diet for BW maintenance or ad libitum and feeding periods up to 21 d suggest mass of the GIT and liver to be sole or primary determinants. However, Kelly et al. (1993) noted a higher rate of in vitro oxygen consumption per unit of tissue DM in ruminal papillae of steers fed A than bromegrass hay. Therefore, differences among treatments of the present experiment in mass of metabolically active tissues should be viewed as grossly indicative of differences in energy and nutrient use. In addition, because most energy is consumed by epithelial tissue rather than by muscle of the GIT (Von Engelhardt and Hales, 1977; Britton and Krehbiel, 1993), GIT tissue with a high proportion of epithelium would consume more energy than that with a lower proportion.

Visceral tissue mass expressed relative to digestible OM intake provides insight as to the proportion of absorbed energy consumed by visceral tissues. For example, a dietary treatment increasing digestible OM intake without affecting GIT and (or) liver mass relative to digestible OM intake would affect peripheral energy availability relatively less than a treatment similarly increasing digestible OM intake but decreasing GIT and (or) liver mass as a proportion of digestible OM intake. Tissue mass also can be scaled to empty BW. However, with normal growth and increasing empty BW, the GIT decreases as a percentage of empty BW at a rate greater than for other tissues such as the liver (Poland, 1991). Hence, the effect of a dietary treatment on visceral tissue mass relative to empty BW is the sum of changes in a number of conditions, including absorptive workload, service functions associated with increased peripheral tissue being accreted and maintained, and mass of all component body tissues.

The difference between B versus A and RW diets in total GIT tissue mass in grams appeared largely a function of lower empty BW with B and, thus, also was related to lower digestible OM intake. Greater ratios of GIT and hepatic tissue mass to digestible OM intake for B diets reflect a greater proportion of absorbed energy used for splanchnic tissue metabolism compared with higher quality forage sources of A and RW. Similar findings were noted by Sun et al. (1994) via measurement of visceral tissue mass with legume and tropical and temperate grass diets, and by Patil et al. (1995) and Goetsch et al. (1996a) through quantification of splanchnic tissue oxygen consumption with tropical and temperate grasses. A stimulatory effect on GIT tissue mass or oxygen consumption of high GIT digesta mass, characteristic of tropical grass diets (Sun et al., 1994; Kouakou et al., 1995) and as also observed in the present experiment, was proposed in these previous studies.

It is unclear what factor associated with A consumption elicited the greatest proportion of epithelium in the reticulo-rumen among forage sources, although perhaps the difference in digestible OM intake between A and other forage sources had an impact different from that between RW and B. Nonetheless, because most energy consumption by the GIT occurs in epithelial tissue, proportions of epithelial tissue and whole tissue mass in the present experiment indicate that energy consumed by the stomach was greater for A than for RW or B diets.

Effects of grain inclusion and nonzero level on GIT mass relative to empty BW and digestible OM intake indicate involvement of factors other than

simply increasing tissue mass with increasing empty BW. Identification of responsible factors is not possible from data of this experiment. Nonetheless, because characteristics of digesta in the GIT such as its mass can alter tissue properties including mass (Rompala et al., 1988; Rompala et al., 1990), the lower quantity of digesta in the gut with than without grain may have had impact. An additional or alternate explanation applicable to the effect of grain inclusion on GIT tissue mass relative to empty BW and digestible OM intake, and also relevant to liver mass as a percentage of digestible OM intake, is dilution of maintenance energy costs; splanchnic tissues of animals consuming forage ad libitum may maintain an excess of metabolic machinery relative to the quantity of nutrients actually being absorbed, perhaps for capacity to respond rapidly to increased energy absorption.

Grain treatment did not interact with forage source in GIT mass in grams or as a proportion of empty BW or digestible OM intake. Thus, effects of dietary grain inclusion on mass of, and energy consumption by, the GIT would have greater impact on energy presented to the liver relative to that with all-forage diets with consumption of forages yielding low versus high digestible OM intake. Furthermore, grain inclusion effects that were of similar absolute magnitude with the different feeding period lengths also indicate that change relative to GIT energy release for all-forage diets would be greater with low BW and digestible OM intake compared with higher BW and digestible OM intake.

Digestible OM intake represents a major component of physiological workload for the liver and, hence, accounted for appreciable variability in liver mass ($r = 0.80$; $P < 0.01$). Mass of the GIT also correlated with liver mass ($r = 0.85$; $P < 0.01$), and explained variation in liver mass was increased by inclusion of both digestible OM intake and total GIT mass in a regression ($R^2 = 82\%$). Thus, a considerable portion of variability in liver mass not accounted for by digestible OM intake was attributable to GIT mass, perhaps because of the high metabolic activity of the GIT and interrelationships between hepatic and GIT metabolism (Bergman and Pell, 1984). These results are quite similar to those of Kouakou et al. (1995), although in the present experiment 59 and 41% of explained variability in liver mass was accounted for by total GIT mass and digestible OM intake, respectively, compared with 74 and 26% noted by Kouakou et al. (1995).

The manifestation of greater digestible OM intake for RW versus B in empty BW largely accounts for the difference in liver mass in grams. However, greater liver mass as a percentage of empty BW for A versus RW and similar liver mass relative to digestible OM intake for A and RW infers influences on liver mass of factors not measured in this experiment, such as the array of available nutrients. For example, generally greatest digestible N intake among forage sources for A along with extensive ruminal degradation of A protein presumably was associated with a high quantity of energy use by the liver to form urea from absorbed ammonia (Reynolds, 1992). In support, when Patil et al. (1996) included A at 0, 20 or 40% of grass diets consumed by sheep, splanchnic tissue oxygen consumption relative to digestible energy intake was not changed despite increased digestible OM intake because of increased hepatic oxygen consumption, which could be partially attributed to elevated ureagenesis. In addition, in the present experiment perhaps generally greater BW gain being supported and empty BW mass being maintained for A versus B and RW diets reflect greater metabolic demands for service functions of the liver with A that are not fully depicted by differences in digestible OM intake. In regards to this latter possibility, that similar findings were not observed for dietary grain inclusion, which also increased digestible OM intake and empty BW, is not supportive. Although, it is possible that compensatory or counteracting factors existed with grain inclusion, such as decreases in GIT tissue mass relative to digestible OM intake and empty BW or an effect of supplemental grain on composition of accreted peripheral tissue (Galloway et al., 1996) that influenced energy used by the liver in service functions.

5. Summary

The greater proportion of epithelium in reticuloruminal tissue and greater liver mass relative to empty BW for A than for B or RW suggest that splanchnic tissue metabolism would not contribute to

a difference in peripheral energy and nutrient availability greater than expected based on digestible OM intake. Mass of the GIT and liver for B diets was lower than for A and RW diets, in accordance with lower empty BW and digestible OM intake. However, greater GIT and hepatic tissue mass relative to digestible OM intake for B versus A and RW reflects a greater proportion of absorbed energy consumed in splanchnic bed function. Thus, energy available to peripheral tissues with low-quality forages such as this B compared with higher quality forages may be even less than anticipated based on digestible OM intake. Decreased GIT and liver mass relative to digestible OM intake with dietary grain inclusion imply greater effects on peripheral energy availability than projected based on the increase in digestible OM intake. In general, few effects of non-zero grain level were observed, indicating that BW gain for diets consisting of various levels of grain should follow differences in digestible OM intake, which in this experiment were nonsignificant, and by change in efficiency of peripheral tissue metabolism. Grain inclusion effects on GIT and liver mass were of similar absolute magnitude regardless of forage source or length of the feeding period, indicating that change in peripheral energy availability relative to that without dietary grain would decrease with increasing forage quality and feeding period length as digestible OM intake increases.

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